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A NEW SPECIES OF *PORPHYRIO* (AVES: RALLIDAE) FROM ARCHEOLOGICAL SITES IN THE MARQUESAS ISLANDS

David W. Steadman

Abstract.—A new species of gallinule, *Porphyrio paepae,* is described from bones found in archeological sites on Hiva Oa and Tahuata, Marquesas Islands. This gallinule represents the only species of *Porphyrio* in the Pacific east of Samoa, Tonga, and Niue, where *P. porphyrio* occurs today. The occurrence of a species of *Porphyrio* in the Marquesas Islands, at the northeastern edge of Polynesia, suggests that congeners may have occurred through much of eastern Polynesia in prehistoric times.

Bones from Polynesian archeological sites have shown that the avifaunas of individual islands were much richer in species before human colonization. Here I describe a new species of gallinule of the genus *Porphyrio* from archeological sites on Hiva Oa and Tahuata islands in the Marquesas. The sites on Hiva Oa were described by Bellwood (1972, 1979:331–337) and Sinoto (1979). The site on Tahuata was excavated recently by B. Rolett, whose studies are in progress. The extinct landbirds from sites on both islands are reviewed briefly by Steadman (in press) and include new species of parrots (Steadman & Zarriello, 1987).

Materials and methods.—Comparative skeletons are from the Division of Birds, USNM. Aside from those of *Porphyrio* (see Tables 1–4), skeletons of *Gallirallus philippensis, Gallirallus owstoni, Gallicrex cinerea, Gallinula chloropus,* and *Fulica atra,* as well as fossils of undescribed species of *Gallirallus* from the Marquesas and elsewhere, were examined to determine generic relationships. Abbreviations: BPBM = Bernice P. Bishop Museum; USNM = National Museum of Natural History, Smithsonian Institution; yr B.P. = corrected radiocarbon years before present. Osteological terminology usually follows that of Baumel et al. (1979). Measurements were taken with dial calipers with 0.05 mm increments, rounded to the nearest 0.1 mm.

Systematic Paleontology

Class Aves
Order Gruiformes
Family Rallidae
Genus *Porphyrio*

Following Olson (1973:409), I regard the genus *Porphyrio* to include "*Porphyrula*" and "*Notornis.*" The fossil material is referred to *Porphyrio* rather than to other large rails (*Gallirallus, Gallicrex, Gallinula, Fulica*) because of the following characters. Carpometacarpus—processus pisiformis extends farther cranially; fovea carpalis caudalis deeper; great distance from processus pisiformis to departure of os metacarpi majus and os metacarpi minus; short distal symphysis of os metacarpi majus and os metacarpi minus. Synsacrum—stout overall; strongly bent ventrally in caudal portion. Femur—more obtuse angle formed at the junction of the impressiones obturatoriae and trochanter femoris; similar size and position of the impressiones iliotrochanteria and linea intermuscularis caudalis; medial margin of the condylus medialis oriented roughly parallel to the shaft rather than diagonal. Tibiotarsus—deep sulcus

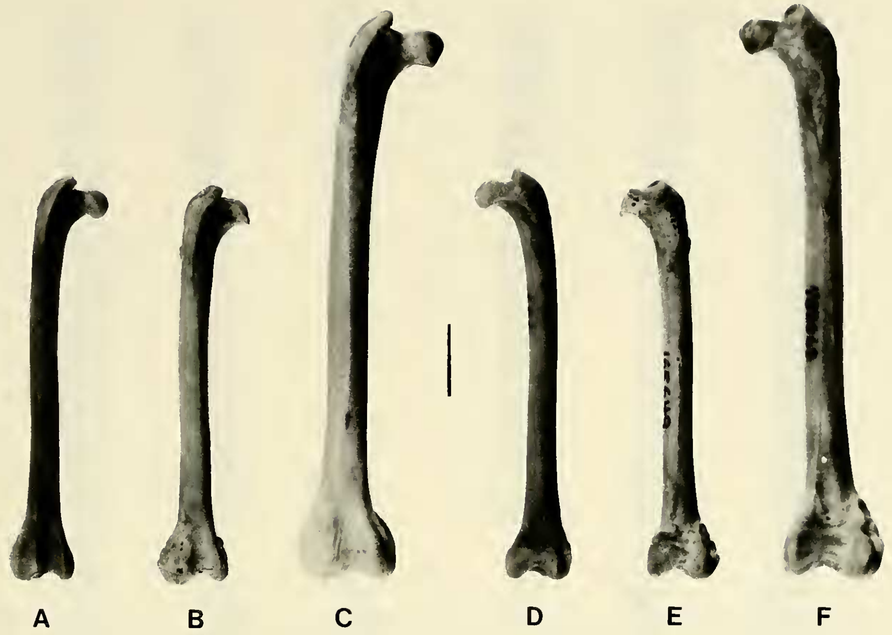

Fig. 1. The femur of *Porphyrio* in cranial (A–C) and caudal (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* holotype, BPBM 165649, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

musculo fibularis; sharp cranio-medial and cranio-lateral margins of the shaft; deep incisura intercondylaris. Tarsometatarsus—extremely thin proximo-medial portion of shaft; more distinct fossa metatarsi. Pedal phalanx—more elongate.

Porphyrio paepae, new species
Figs. 1–4

Holotype.—Femur lacking only the medial portion of facies articularis acetabularis, BPBM 165649, from Hanatekua Shelter No. 2 Site (MH3-12), square E2-F2, 100–140 cm, Hiva Oa, Marquesas Islands, 19 Dec 1967, P. Bellwood. (This site has been referred to as Hanatukua, with an earlier Bishop Museum site designation of MH-11.)

Paratypes.—Hiva Oa, 1967, P. Bellwood: Pelvis—BPBM 165656, Hanatekua Shelter No. 2 Site (MH3-12), square D1, 80–100 cm. Femur (tentatively referred)—BPBM 168539, Hanatekua Beach Site (MH3-13, formerly designated MH-12), test pit 24, 40+ cm. Four tibiotarsi—BPBM 165651, Hanatekua Shelter No. 2 Site (MH3-12), square E1-H1, layer 10 (section collapse); BPBM 165652, Hanatekua Beach Site (MH3-13), test pit 2, layer 4; BPBM 167496, Hanatekua Beach Site (MH3-13), test pit 22, layer 4, 40+ cm; BPBM 165654, Hanaui Site (MH-22), test pit 8. Two tarsometatarsi—BPBM 165650, Hanatekua Shelter No. 2 Site (MH3-12), square E2-F2, 100–150 cm; BPBM 165653, Hanatekua Beach Site (MH3-13), test pit 23, 30+ cm.

Tahuata, Hanamiai Site (MT1), 1985, B. Rolett: Carpometacarpus—BPBM 166427, square L11, layer I37. Synsacrum—BPBM 166432, square L10, layer G/H16 (240–250 cm). Four femora—BPBM 166434, square I12, layer G/H14 (230–240 cm); BPBM 166430, square L11, layer I36; BPBM 166426, square L11, layer I37; BPBM 166424, square K9, layer F10 (180+ cm).

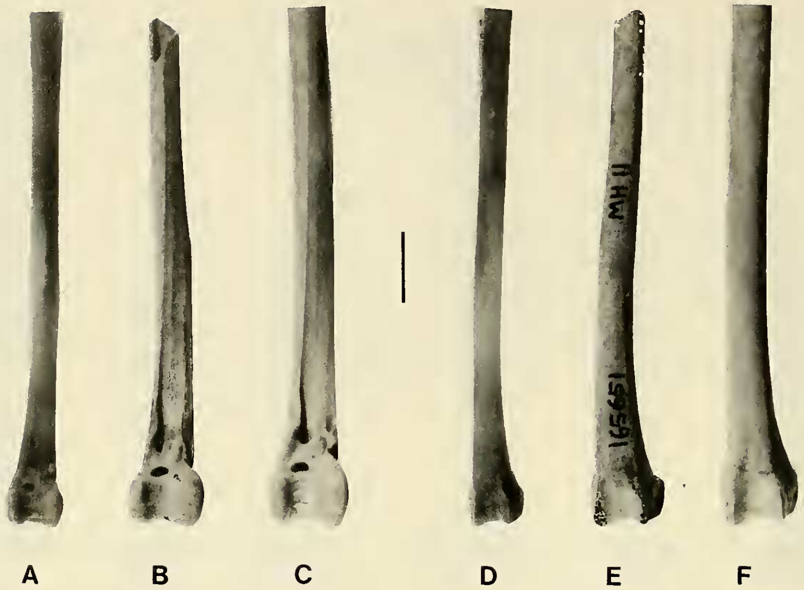

Fig. 2. The tibiotarsus of *Porphyrio* in cranial (A–C) and caudal (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 165651, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

Two tibiotarsi—BPBM 166428, square M13, layer H31 (255–260 cm); BPBM 166433, square N13, layer H33 (260–265 cm). Two tarsometatarsi—BPBM 166429, square K11, layer G/H16 (220–230 cm); BPBM 166425, square K10, layer G13 (220–230 cm).

Diagnosis.—Smaller than any species of *Porphyrio* except the "*Porphyrula*" group (*P. martinica, P. alleni, P. flavirostris*) (Tables 1–4). Carpometacarpus: short; os metacarpi minus and os metacarpi majus fused proximally for a greater distance. Femur: shaft broader than in *P. martinica*; shaft straighter than in *P. porphyrio, P. poliocephalus,* or *P. pulverulentus*; sulcus patellaris broader than in *P. martinica*; impressio ligamentum cruciati caudalis deeper than in *P. martinica*; in medial aspect, condylus medialis joins caudal surface of the shaft nearly perpendicularly (more obtuse angle in all others); in lateral aspect, the proximal margin of crista trochanteris less rounded than in *P. porphyrio.* Tibiotarsus: shaft relatively shallower than in *P. porphyrio*; incisura intercondylaris relatively broader and deeper than in all others; proximal portion of condylus lateralis more rounded and joins the shaft more perpendicularly (an obtuse angle is formed in all others).

Etymology.—From the Marquesan word *paepae,* which is a prehistoric rectangular stone platform that served as a base for various dwellings (Bellwood 1979:333 and fig. 12.3). Like the extinct gallinule described here, the *paepae* is no longer an active part of Marquesan culture, although its remains are scattered on the islands.

Remarks.—No skeletons were available for *Porphyrio alleni* of Africa or *P. flavirostris* of South America. The former is about the size of *P. martinica,* while the latter is smaller than *P. martinica.*

Discussion

The chronology of the Hanatekua Shelter No. 2 Site is poorly defined, although the bones of *Porphyrio paepae* from this site may be from pre-cultural levels (Y. H. Sin-

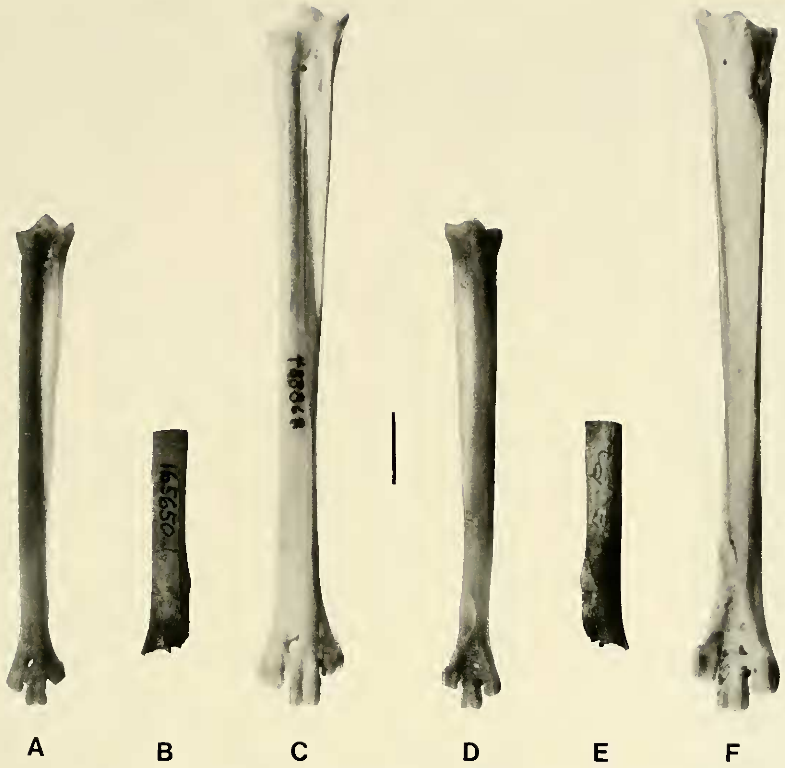

Fig. 3. The tarsometatarsus of *Porphyrio* in dorsal (A–C) and plantar (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 165650, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

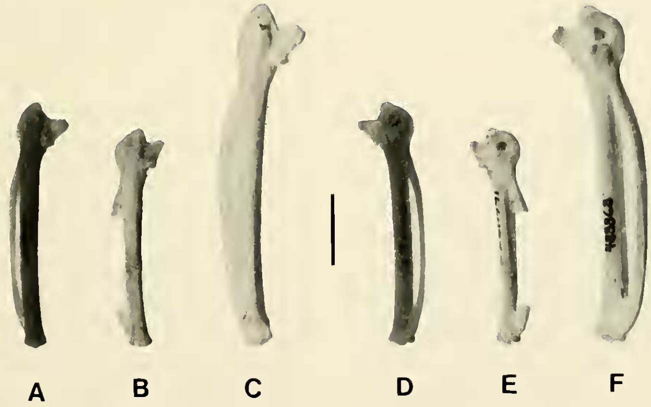

Fig. 4. The carpometacarpus of *Porphyrio* in dorsal (A–C) and ventral (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 166427, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

Table 1.—Measurements (in mm) of the carpometacarpus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Total length	Proximal width	Proximal depth	Least depth of shaft
Porphyrio paepae	29.3	6.8	3.6	2.1
Tahuata, Marquesas (U)	1	1	1	1
BPBM 166427				
Porphyrio porphyrio	45.2	9.5	4.8	3.0
Bechuanaland (M)	1	1	1	1
USNM 488868				
Porphyrio porphyrio	—	10.5	4.9	—
New Caledonia (M)		1	1	
USNM 561547				
Porphyrio porphyrio	47.1	10.0	4.8	3.6
New Caledonia (F)	47.0–47.2	9.9–10.0	4.8	3.5–3.7
USNM 561549, 561551	2	2	2	2
Porphyrio porphyrio	52.4	10.8	5.0	3.9
Captive (M) USNM	52.0–52.9	10.8–10.9	4.9–5.2	3.9
555504, 557529	2	2	2	2
Porphyrio poliocephalus	43.5	9.5	4.4	2.8
Thailand (F)	1	1	1	1
USNM 343212				
Porphyrio poliocephalus	54.5	11.5	5.3	3.6
Captive (M) USNM 491890	1	1	1	1
Porphyrio poliocephalus	43.5	10.0	4.3	3.4
Captive (F) USNM 347372	1	1	1	1
Porphyrio pulverulentus	47.0	10.0	4.7	3.4
Philippines (M, U)	46.5–47.4	9.9–10.2	4.6–4.8	3.3–3.5
USNM 200817, 226035	2	2	2	2
Porphyrio martinica	32.6	7.1	3.4	2.1
Florida (M)	31.6–33.1	6.8–7.5	3.2–3.5	2.0–2.2
USNM 501122, 501126, 501128, 501129, 501131	5	5	5	5
Porphyrio martinica	30.8	6.6	3.2	2.1
Florida (F) USNM	30.6–31.3	6.3–6.9	3.0–3.4	2.0–2.3
501123–501125, 501130	4	4	4	4

oto, pers. comm.). Kirch (1986:25) reported a radiocarbon date of 1930 ± 80 yr B.P. for Hanatekua Shelter No. 2, although I am not sure how this date relates stratigraphically to the fossils of *P. paepae.* The chronology of the Hanamiai Site on Tahuata is currently being resolved and lies mainly in the range of 1500 to 800 yr B.P. (B. Rolett, pers. comm.). All bones of *P. paepae* from Hanamiai are associated with Polynesian artifacts from the lowest cultural levels.

The only other large rails from the Marquesas are extinct, undescribed, flightless species of *Gallirallus* from Ua Huka, Nuku Hiva, Hiva Oa, and Tahuata. The wing elements in these species are much smaller than those in any species of *Porphyrio,* including *P. paepae.* Based upon the size and morphology of the carpometacarpus, *P. paepae* had somewhat reduced powers of flight compared to congeners, yet probably was not flightless. A crude indication of volancy is presented in Table 5 by the ratio of the total lengths of the carpometacarpus and femur (the only wing or leg bones known in *P. paepae* for which the total length could

Table 2.—Measurements (in mm) of the femur of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Total length	Depth of proximal end	Least width of shaft	Least depth of shaft	Width of distal end	Depth of condylus medialis
Porphyrio paepae	52.5	7.7	3.9	4.0	9.5	7.0
Hiva Oa, Marquesas (U)	1	1	1	1	1	1
Holotype BPBM 165649						
Porphyrio paepae	51.7+	—	4.2	4.3	9.5+	—
Tahuata, Marquesas (U)	1		4.1–4.2	4.2–4.4	1	
BPBM 166430, 166434			2	2		
Porphyrio porphyrio	81.1	12.3	5.9	5.8	13.0	9.9
New Caledonia (M)	1	1	1	1	1	1
USNM 561547						
Porphyrio porphyrio	72.6	10.9	5.3	5.5	13.8	10.0
New Caledonia (F)	72.4–72.8	10.9	5.2–5.4	5.4–5.6	1	1
USNM 561549, 561551	2	2	2	2		
Porphyrio porphyrio	74.5	10.1	5.1	5.0	12.6	9.6
Bechuanaland (M)	1	1	1	1	12.3–12.9	9.6–9.7
USNM 488868					2	2
Porphyrio porphyrio	76.8	11.2	5.9	5.8	13.5	11.3
Captive (M)	73.8–79.8	11.0–11.4	5.8–6.0	5.7–6.0	13.3–13.7	11.2–11.4
USNM 555504, 557529	2	2	2	2	2	2
Porphyrio poliocephalus	68.8	9.3	4.8	4.3	11.7	9.8
Thailand (F)	1	1	1	1	1	1
USNM 343212						
Porphyrio poliocephalus	76.2	11.3	5.5	5.7	13.2	10.8
Captive (M) USNM	62.7–83.7	8.9–12.5	4.4–6.3	4.4–6.5	10.8–14.6	8.8–12.0
318498, 344474, 491890	3	3	3	3	3	3
Porphyrio poliocephalus	67.0	9.6	4.6	4.4	11.3	9.2
Captive (F) USNM	64.6–70.7	9.1–9.9	4.5–4.7	4.2–4.6	10.9–11.8	8.7–9.4
289454, 321151, 347372	3	3	3	3	3	3
Porphyrio poliocephalus	69.0	9.2	4.8	5.2	12.0	9.4
Captive (U)	61.2–76.8	1	4.4–5.1	4.6–5.7	10.8–13.3	8.1–10.8
USNM 19761, 227119	2		2	2	2	2
Porphyrio pulverulentus	78.2	11.2	5.2	5.9	13.8	11.1
Philippines (M)	77.9–78.4	11.0–11.4	5.1–5.3	2	13.4–14.2	10.5–11.7
USNM 226035, 292297	2	2	2		2	2
Porphyrio pulverulentus	75.4	10.8	5.1	5.6	13.4	10.8
Philippines (F)	1	1	1	1	1	1
USNM 292296						
Porphyrio martinica	54.2	7.0	3.6	3.8	8.5	7.0
Florida (M) USNM	52.8–55.4	6.7–7.2	3.4–3.7	3.6–3.9	8.1–8.7	6.7–7.2
501122, 501126, 501128,	4	5	5	5	5	4
501129, 501131						
Porphyrio martinica	50.7	6.6	3.4	3.5	7.9	6.6
Florida, Louisiana,	47.7–52.4	6.1–7.2	3.2–3.6	3.2–3.8	7.4–8.8	6.1–7.1
Dominican Republic (F)	6	6	6	6	6	6
USNM 288205, 499438,						
501123–501125, 501130						

Table 3.—Measurements (in mm) of the tibiotarsus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown. PE = proximal end. PS = pons supratendineus.

	Least width of shaft	Width of shaft at PE of PS	Least depth of shaft	Distal width	Height of condylus medialis	Height of condylus lateralis	Depth of condylus medialis	Depth of condylus lateralis
Porphyrio paepae	4.0	6.4	3.4	9.8	5.8	8.2	9.6	8.9+
Hiva Oa (U) BPBM	3.7–4.2	6.1–6.7	3.3–3.5	1	1	1	1	1
165651, 165652,	3	2	4					
165654, 167496								
Porphyrio paepae	—	5.8	3.4	8.6+	5.4+	7.3	8.5+	8.3
Tahuata (U) BPBM		5.7–6.0	3.4	1	1	1	1	1
1664228, 166433		2	2					
Porphyrio porphyrio	5.1	7.2	3.8	10.2	6.0	9.1	10.5	10.2
Bechuanaland (M)	1	1	1	1	1	1	1	1
USNM 488868								
Porphyrio porphyrio	6.0	8.1	4.8	11.1	7.0	9.8	11.6	11.3
New Caledonia (M)	1	1	1	1	1	1	1	1
USNM 561547								
Porphyrio porphyrio	5.6	7.6	4.3	10.4	6.4	9.2	11.0	10.4
New Caledonia (F)	5.4–5.9	7.4–7.8	4.3	10.3–10.5	6.3–6.4	9.2–9.3	10.8–11.1	10.2–10.5
USNM 561549, 561551	2	2	2	2	2	2	2	2
Porphyrio porphyrio	—	7.7	—	10.6	6.3+	9.9	10.9+	10.6+
Tikopia, Solomon Is.		1		1	1	1	1	1
BPBM 166227, 166263								
Porphyrio porphyrio	5.7	8.6	4.6	11.6	6.8	10.2	12.0	11.2
Captive (M)	5.5–5.9	8.3–8.9	2	11.5–11.8	6.8–6.9	10.2–10.3	11.9–12.1	10.9–11.5
USNM 555504, 557529	2	2		2	2	2	2	2
Porphyrio poliocephalus	4.4	6.6	3.5	9.2	5.6	8.2	9.9	9.2
Thailand (F)	4.3–4.6	6.4–6.7	3.4–3.6	9.1–9.2	5.3–5.9	8.0–8.3	9.6–10.2	2
USNM 343212, 343213	2	2	2	2	2	2	2	
Porphyrio poliocephalus	5.2	7.6	4.0	10.6	6.2	9.0	11.1	10.0
Captive (M)	4.5–5.8	6.8–8.5	3.4–4.6	9.1–12.0	5.3—7.1	7.8–10.3	9.2–13.0	8.6–11.3
USNM 344474, 491890	2	2	2	2	2	2	2	2
Porphyrio poliocephalus	4.8	6.8	4.0	9.7	6.0	8.4	10.0	9.4
Captive (F)	4.7–4.9	6.5–7.1	3.6–4.3	1	2	8.1–8.6	1	9.3–9.4
USNM 321151, 347372	2	2	2			2		2
Porphyrio pulverulentus	5.5	7.8	4.2	11.2	6.5	10.0	11.4	10.7
Philippines (M, U)	5.4–5.6	7.7–7.9	4.1–4.4	2	6.3–6.7	9.9–10.1	11.0–11.8	10.5–10.9
USNM 200817, 226035	2	2	2		2	2	2	2
Porphyrio martinica	3.5	5.0	2.7	7.1	4.3	6.2	7.0	6.9
Florida (M)	3.3–3.7	4.8–5.4	2.6–2.9	6.9–7.5	4.1–4.7	6.1–6.4	6.9–7.3	6.8–7.1
USNM 501122, 501126,	5	5	5	5	5	5	5	5
501128, 501129, 501131								
Porphyrio martinica	3.4	4.9	2.6	6.8	4.2	6.0	6.7	6.6
Florida, Louisiana,	2.8–3.6	4.7–5.1	2.5–2.8	6.3–7.5	3.9–4.4	5.8–6.3	6.1–7.0	6.2–7.1
Dominican Republic (F)	6	6	6	6	6	6	6	6
USNM 288205, 499438,								
501123–501125, 501130								

be determined). Although the value of this ratio is less in *P. paepae* than in other congeners, the difference is small and might be of little significance, especially because the fossils are of unknown sex. Note also that the skeletons of captive individuals of *P. porphyrio* and *P. poliocephalus* have higher ratios than those of wild individuals. For

Table 4.—Measurements (in mm) of the tarsometatarsus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Minimum width of shaft	Minimum depth of shaft	Proximal width	Width of hypotarsus
Porphyrio paepae	4.9	2.9	—	—
Hiva Oa, Marquesas (U)	1	1		
BPBM 165650				
Porphyrio paepae	—	—	10.4	5.1
Tahuata, Marquesas (U)			1	1
BPBM 166425				
Porphyrio porphyrio	5.0	3.6	10.9	5.4
Bechuanaland (M)	1	1	1	1
USNM 488868				
Porphyrio porphyrio	—	3.9	11.8	5.8
New Caledonia (M)		1	1	1
USNM 561547				
Porphyrio porphyrio	5.5	3.6	10.9	5.4
New Caledonia (F)	5.4–5.6	3.6–3.7	10.8–11.0	5.3–5.5
USNM 561549, 561551	2	2	2	2
Porphyrio porphyrio	—	3.7	—	5.6
Tikopia, Solomon Is. (U)		1		1
BPBM 166228, 166230				
Porphyrio porphyrio	5.9	4.2	12.4	5.8
Captive (M)	5.7–6.1	4.1–4.2	12.3–12.5	5.8–5.9
USNM 555504, 557529	2	2	2	2
Porphyrio poliocephalus	4.6	3.2	9.9	4.7
Thailand (F) USNM 343212	1	1	1	1
Porphyrio poliocephalus	6.5	4.3	12.4	6.3
Captive (M) USNM 491890	1	1	1	1
Porphyrio poliocephalus	5.2	3.3	10.4	5.0
Captive (F) USNM 347372	1	1	1	1
Porphyrio pulverulentus	5.5	3.8	11.6	6.0
Philippines (M, U)	5.1–5.9	3.7–4.0	11.5–11.6	6.0–6.1
USNM 200817, 226035	2	2	2	2
Porphyrio martinica	3.8	2.5	7.6	4.0
Florida (M)	3.7–3.9	2.3–2.6	7.3–7.9	3.8–4.3
USNM 501122, 501126, 501128, 501129, 501131	5	5	4	4
Porphyrio martinica	3.6	2.5	7.0	3.6
Florida (F)	3.2–3.9	2.4–2.6	6.7–7.2	3.4–3.7
USNM 501123–501125, 501130	4	4	4	4

this and other reasons, I do not consider the captive individuals to be an absolutely accurate representation of either the quantitative (Tables 1–5) or qualitative characters of *P. porphyrio* or *P. poliocephalus.* The diagnosis is based only upon wild individuals. In all of the tables, the values for *P. martinica* provide the best assessment of the intraspecific variation of wild populations.

Balouet & Olson (in press) have described a flightless, extinct species of *Porphyrio* from late Holocene fossils from New Caledonia. This new species was much larger even than *P. porphyrio,* which is the only other congener in the Pacific, other than the large, flightless species on New Zealand ("*Notornis*") and the historically extinct *P. albus* of Lord Howe Island, which was similar in size

Table 5.—Ratio of total lengths: carpometacarpus divided by femur, expressed as a percentage. From data in Tables 1 and 2.

Porphyrio paepae	56.7 (−)
Tahuata, Marquesas (U)	1
BPBM 166427, 166434	
Porphyrio paepae	55.8
Tahuata and Hiva Oa, Marquesas (U)	1
BPBM 166427, 165649	
Porphyrio porphyrio	60.7
Bechuanaland (M)	1
USNM 488868	
Porphyrio porphyrio	64.8
New Caledonia (F)	64.6–65.1
USNM 561549, 561551	2
Porphyrio porphyrio	68.4
Captive (M)	66.3–70.5
USNM 555504, 557529	2
Porphyrio poliocephalus	63.2
Thailand (F) USNM 343212	1
Porphyrio poliocephalus	66.3
Captive (M) USNM 491890	1
Porphyrio pulverulentus	60.4
Philippines (M)	1
USNM 226035	
Porphyrio martinica	60.6
Florida (4M, 4F)	58.4–62.7
USNM 501122–501126, 501128, 501130, 501131	8

to *P. porphyrio* but had smaller wings. In the Pacific, *P. porphyrio* occurs from the New Guinean region east through Melanesia to the western Polynesian islands of Tonga, Samoa, and Niue; it has not been recorded, either living or as a fossil, from eastern Polynesia. Thus *P. paepae* represents an eastward range extension of 3200 km for the genus. Because *Porphyrio* once inhabited the Marquesas Islands, at the northeast corner of Polynesia, it is likely that fossils of these gallinules will be discovered elsewhere in eastern Polynesia.

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Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230.